THE RATE OF EVOLUTION

By Professor EDWIN GRANT CONKLIN

THE results of evolution as contrasted with its causes may be considered from three different aspects which may be characterized briefly as diversity, adaptation and progress. The first concerns increasing diversification as shown in the appearance of varieties, species and genera which are no more complex in organization than the forms from which they have descended and which may be less complex; such changes which do not lead to more highly organized forms may be known as variation, speciation or diversification. A second aspect of evolution deals with increasing adaptation to conditions of life; this may or may not be associated with progressive organization or with speciation and may be called progressive adaptation. A third aspect, and most important as measured by its results, concerns the advance in organization from the simplest to the most complex organisms; this may be called progressive evolution, or more briefly progress. No doubt progressive organization, by which is meant increasing differentiation and integration has come about through diversification or speciation but on the other hand the latter has only rarely led to the former.

I. DIVERSITY

The most evident phase of evolution and the one which has been dealt with exclusively by the experimental method is diversification. Smaller differences or variations among organisms may be classified, according to their mode of origin as (*a*) Fluctuations, (*b*) New Combinations, (*c*) Mutations.

1. *Fluctuations or Modifications.*—Fluctuations are variations whose differential causes are environmental, they come and go with changing environment; they are modifications of the soma rather than of the germplasm, of individual development rather than of heredity. They can be distinguished from heritable variations by the fact that they are not permanent. They are probably more numerous than all other diversities, their number and extent being proportional to the number and degree of the environmental changes which called them forth. They rarely if ever lead to modifications of the germplasm and are therefore of little or no evolutionary value.

2. *New Combinations of Mendelian Factors.*—The most common kind of inherited diversity is due to new combinations of inheritance factors in sexual reproduction. The segregation of genes in different germ cells and their combination in fertilization are rarely exactly the same in two instances. In the case of animals and plants where self fertilization does not occur there are usually several "contrasting characters" or allelomorphs in the parents, and the number of possible combinations of these rises rapidly with each additional pair of allelomorphs until in species crosses where there are many allelomorphs there may be as many different combinations as there are individuals in the F_2 generation. Furthermore the number of such new combinations is proportional to the number of germ cells which unite in fertilization and to the number of chromosomes in those germ cells. Therefore the rate at which such new combinations are formed must depend upon the rate of reproduction and the number of chromosomes and allelomorphs.

A certain proportion of these combinations are homozygous and breed true, but most of them are heterozygous and show Mendelian splitting in subsequent generations. Bateson says that most of the new varieties of cultivated plants are the results of deliberate crossing. This is the method which Burbank has employed with such wonderful success in the production of his "new creations in plant life." Linnean species contain many different biotypes and by crossing these many new combinations are produced, some of which may be economically valuable. If individuals showing desired combinations are interbred it is usually possible after a few generations to get homozygotes that breed true and thus a new variety or breed is established.

Such new combinations may therefore be of evolutionary value. It is probable that certain species of domestic animals and plants are of hybrid origin; among these are dogs, cats, cattle, horses, sheep, pigs, poultry, wheat, oats, rice, plums, cherries, etc. More than one thousand different plant hybrids have been described as occurring in nature but many of these are heterozygotes and do not breed true. Lotsy maintains that hybridization is the most important cause of evolution, but hybridization implies existing diversities such as dominants and recessives. Where and how did these arise? To attribute these diversities to still earlier hybridization only puts off the question of their *origin.*

3. *Mutants or Elementary Species.*—Since the publication

in 1901 of deVries' great monograph on the "Mutation Theory" the superlative importance of mutations in evolution has been widely accepted. Genuine mutants, due most probably to sudden changes in individual genes, have now been found in so large a number of plants and animals among both wild and domesticated species, that it seems probable that all inherited differences appeared *in the first instance* in this way.

The evidence is accumulating that mutations are rare only when contrasted with the relatively large number of individuals which show no hereditary variations. Wherever there are contrasting characters, or allelomorphs, and few things are more common, a mutation has occurred at some time, though it may have been long ago, by which these allelomorphs became different. Wherever there are breeds, races, or stocks there is evidence, *ex hypothese,* that their constant differences were established by one or many mutations occurring at some time or times in the past.

The rate at which mutations appear seems to differ greatly in different species, but it is suggestive that they are found most abundantly in species which have been studied most thoroughly, and it is probable that they are of much more frequent occurrence than is now known. The largest number of mutants which have been found in any species under conditions of accurate observation and experiment are in the pomice fly *Drosophila melanogaster,* and one of the most frequent types of mutation in this species is the appearance of lethal factors which cause the early death of individuals which receive this lethal from both parents.

Muller and Altenburg find in *Drosophila* that the ratio of lethal mutants to the normal condition in the X-chromosome varies from 1:30 to 1:53 depending on the temperature, and if mutations occur in other chromosomes at the same rate as in the X-chromosome, a new lethal mutation in one or another chromosome occurs in about 1 fly out of 13. They further argue that since a sex-linked lethal mutation appears in about one fly in fifty and since there are two X-chromosomes in the female such a mutation would occur in one X-chromosome in about 100 *generations* and, since there are about 25 generations a year, say once in 4 years. It seems probable that there is some confusion in this reasoning since if a mutation occurs in one X-chromosome in every 100 *X-chromosomes* it should appear much more frequently than once in every 100 *generations.*

If mutations are proportional to the number of genes they should be much more numerous in very complex organisms than

in relatively simple ones. It is not evident that this is the case. It is true that most mutations are positively injurious, or at least that they are less beneficial than the typical characters of wild species, and therefore they are eliminated almost as soon as they appear. Consequently such mutations are rarely seen unless they are searched for diligently. In all probability mutations are more numerous and occur more frequently than is now known, but the evidence seems to favor the view that they are more numerous in some species and phyla than in others. Whether they are caused by environmental conditions and are therefore proportional in number to environmental changes is at present unknown, although Muller and Altenburg indicate that they occur more frequently at high temperatures than at lower ones.

4. *Species* are presumably the result of the heaping up of viable mutations. The term "species" is an indefinite one and is not everywhere used in precisely the same sense. Nevertheless a very casual survey of the living world shows that some groups of animals and plants have undergone very much more extensive diversification than other groups. If we consider merely the approximate number of known spceies both living and extinct in different phyla of the animal kingdom we find very great differences as is shown by the following table of the approximate number of species in the principal animal phyla:[1]

Protozoa	8,000
Sponges	2,500
Cœlenterata	4,500
Platyhelminthes	5,000
Nemathelminthes	1,500
Rotifera	500
Polyzoa	1,700
Annelida	4,000
Arthropoda	400,000
Mollusca	61,000
Echinodermata	4,000
Chordata	36,000

In the different classes of Arthropods there are:

Crustacea	16,000
Arachnida	16,000
Myriopoda	2,000
Insects	360,000

In the different classes of Vertebrata the number of known species is about as follows:

[1] See Pratt, H. S., "On the Number of Known Species of Animals," *Science*, N. S., Vol. 35, 1912.

Pisces	13,000
Amphibia	1,400
Reptilia	3,500
Aves	13,000
Mammalia	3,500

These numbers represent merely a crude approximation of the number of known species, both living and extinct. Undoubtedly many more species remain to be discovered and this number will be larger among the Protozoa, for example, than among the Chordata and in the Pisces than in the Mammalia. For our purpose however this crude census of the number of species in different phyla of the animal kingdom and in different classes of the arthropoda and the vertebrata will suffice.

(*a*) It is at once apparent that the number of species in a group is not dependent entirely upon its age. Birds which arose in the Jurassic and are the most recent of vertebrate classes have more than 3 times as many species as mammals which first appeared in the Triassic and are therefore older. There are 100 times as many species of arthropods as of echinoderms though apparently both phyla are of about the same geological antiquity; there are 15 times as many species of mollusks as of annelids and more than 4 times as many species of chordates as of protozoa, although the former represents the most recent and the latter the most ancient phylum of the animal kingdom.

(*b*) Furthermore the number of species is not wholly dependent upon the number of individuals produced nor upon their rate of reproduction, as might be inferred from some of the recent discussions of mutation and natural selection. Protozoa and protophyta probably include vastly more individuals than all other groups of organisms put together and their rate of multiplication is many times greater than in any other group and yet the number of recognized species is relatively small. Chordata are probably poorer in individuals and their rate of reproduction is much slower than echinoderms though they are 9 times as numerous in species. Birds which are relatively few in number of individuals and of eggs produced have as many species as the much older class of fishes which lay perhaps a thousand times as many eggs. If evolution depends upon the chance production of mutations and the sorting of these by natural selection it might be supposed that mutations would be most abundant where fecundity was highest and that fish or starfish or oysters which produce approximately a million eggs a year would evolve much more rapidly than birds which lay only from two to twenty eggs a year: that frogs which lay pos-

sibly 200 eggs a year would evolve more rapidly than mammals which produce only from one to twenty young per year. Even within the same class and family there is no direct correlation between the number of young produced and the number of species, as is shown by a comparison of passerine and gallinaceous birds; in the former group the number of eggs laid is small but there are 5,700 living species, while in the latter where the number of eggs is perhaps from 5 to 10 times as great, there are only 400 living species. In the genus *Crepidula,* a prosobranch gastropod, there are 60 times as many eggs produced by an individual of the species *fornicata* as by one of *convexa* yet individuals and mutations are apparently no more numerous in one species than in the other. In general it seems that *evolution has been more rapid where fewer young are produced and these are better cared for.*

In none of these cases is the smaller number of eggs or of young produced compensated for by a larger number of individuals which are reproducing. To a certain extent the number of individuals in a species is correlated with their size; the smallest of all animals, the protozoa, are the most numerous in individuals, the largest, elephants and whales, are the poorest in individuals, but in comparing the number of species in a group there is no constant correlation between size of individual and rate of reproduction, though in general the smaller animals reproduce more rapidly than the larger ones. On the other hand there is no satisfactory evidence that smaller animals undergo more rapid evolution than larger ones.

(*c*) The rate of evolution is not always dependent upon changes in environment and diversities of habitat. There are more species of marine organisms in the tropics, where the environment is relatively uniform than in temperate regions. Amphibia which inhabit both land and water have only one-tenth as many species as fish which inhabit water alone, and echinoderm species are nearly twice as numerous as sponges, though both are confined entirely or almost entirely to the sea. Undoubtedly, however, there are more chances for the survival of mutations among living things which are able to adapt themselves to many kinds of environment than among those which are confined to a limited medium or habitat. Thus the fact that arthropods are by all odds the most richly diversified phylum in the animal kingdom is probably associated with the fact that they have extended into all media, namely, sea, fresh water, land and air. The echinoderms on the other hand have been confined entirely to the sea probably owing to the fact that be-

cause of inherited constitution they were unable to adapt themselves to other media; accordingly the number of species of echinoderms is much less than that of arthropods. Many paleontologists maintain that the rate and direction of evolution are determined by environmental changes and they describe "waves of evolution" as caused by intermittent changes of environment.

(*d*) If the chances of mutation were equal in all classes of organisms and if mutations represent chance alterations in the structure of the germplasm the number of mutations which appear would be dependent merely upon the number of young produced; but the number of these mutations which survive and give rise to species is undoubtedly limited by the environment, that is by natural selection. Mutations generally are wiped out almost as soon as they appear because they render the organism less viable or because they are not capable of further development, owing either to physico-chemical limitations of the germplasm or to environmental limitations. If this be granted the question still remains *why* are mutations more viable and more promising in some groups than in others?

No satisfactory answer can be given to this question at present but it seems probable that the rate of mutation depends primarily upon the particular organization of the germplasm in different groups of animals and plants. Some types of germplasm may be relatively stable and mutations few in such cases; other types relatively unstable and here mutations may be more numerous. Whether mutations will lead to the formation of species or not will depend in part upon the character and number of the mutations, and in part upon the environment, for the persistence of a mutation must depend upon its finding a suitable place in nature.

II. Adaptation

All kinds of organisms must be fairly well adapted to their conditions of life if they are to survive. The very fact of survival is evidence of adaptation. There is no evidence that protozoa are not as well adapted to their conditions as fishes and birds and mammals are to theirs. We cannot therefore assume that adaptations are less complete in lower forms than in higher ones, but they are certainly less complex and perfect as will be at once apparent when one compares the eye of a jelly fish and that of a fish or bird or man. We have here the same problem that we meet in individual development; germ cells, developing eggs and embryos must be adapted to their conditions of life if

they are to survive, but those conditions and the corresponding adaptations are not so complex as they are in fully developed animals. This increasing complexity and perfection of adaptation from the lowest to the highest forms is part of the problem of progressive evolution and will be considered in the next section.

If adaptations are the result of chance mutations and the elimination of the unfit the rate of adaptation should be proportional to the number of such mutations and the severity of elimination; other things being equal, the number of mutations and the severity of elimination should be proportional to the rate of reproduction; consequently the rate of adaptation should be proportional to the rate of reproduction. There is no evidence that this is true, and when we consider the complexity and perfection of adaptations in higher forms it seems that the reverse is true and that adaptations have gone farther and faster in organisms in which the rate of reproduction and of elimination is relatively low.

III. Progressive Evolution

Thousands of species appear which do not lead to any increase in differentiation or in complexity of organization; they appear and if they find a suitable place in the world they may persist, but most of them do not represent any real progress. Almost all of the mutations which have been studied hitherto are retrogressive in that they represent a simplification of germplasm if not of adult structure and while some of them represent stages in the formation of species few, if any of them, represent a real increase in differentiation. Indeed progressive evolution, as distinct from speciation or adaptation, has apparently halted in almost every group of organisms; usually neither mutations nor real Linnean species lead anywhere except to mere diversity. There are probably more than a million known species of animals and plants both living and extinct and yet there have been relatively few lines of progress.

Whether evolution will lead to increasing complexity of organization or merely to diversification must also depend upon the nature of the germplasm; increasing complexity in evolutionary series must have depended upon rare and fortunate mutations which were not only viable but contained the possibilities of much further evolution and which were peculiarly suited to a favorable place in nature. On the other hand every mutant or species does not represent the beginnings of a new path of evolution probably because it is limited by the con-

stitution of its germplasm so that further progress is rarely possible. The old explanation of the cessation of progressive evolution among protozoa, for instance, was a purely teleological one, namely, they remained protozoa in order that they might occupy a place in nature which would otherwise be unoccupied. The true explanation is more probably that they are incapable of further progressive evolution; they have branched off from the main stem of progress and can not now return. The case is like that of the differentiation of cells in development; the only cells which remain capable of indefinite development are the germ cells; muscle cells and nerve cells can not again become germ cells, and in a similar way the only cells which remain capable of progressive evolution are certain kinds of germ cells in certain groups of organisms. Certain species, like certain cells, have become so highly differentiated in particular lines that they cannot progress much beyond the limits already reached; they are too highly specialized to give origin to new lines of progress.

Paths of Progress

In general progressive evolution implies an increase in the differentiation and integration of parts. In unicellular organisms such increase of organization is seen in the multiplication and differentiation of many minor parts of the cell such as chromomeres, chromosomes, nuclei and the various units and organellae of the cytoplasm. The utmost limits of such progressive organization within the limits of a single cell were reached relatively early in the history of life upon the earth. Living protozoa and protophyta are probably no more complex than those which existed in the Proterozoic Era and certainly there is no reason to suppose that unicellular forms are now undergoing progressive evolution; they ceased long ago to advance in organization and since then they have changed only in the direction of diversification or speciation.

1. *Multicellularity.*—A new path of progress was found when unicellular forms gave rise to multicellular ones. When the protozoan ancestors of the metazoa divided, the daughter cells no longer moved apart, and at the same time these daughter cells retained the differentiations which they had at the time of division and in the course of further evolution added to these differentiations. In this way individual cells and cell aggregates became new units of differentiation and the entire organism, composed of multitudes of such cells, was able to reach a stage of organization which was entirely impossible within a single cell.

A similar transition from a unicellular to a multicellular condition is seen at the present day in the development of an egg. The single egg cell shows certain differentiations, as does also the sperm cell, but these differentiations never go farther than the type of differentiations characteristic of a protozoan. By repeated divisions of the egg, cells are formed which adhere together and the initial differences which these cells have at the time of division are maintained and augmented as the cleavage of the egg proceeds—that is, there is no regulation following division by which each cell replaces lost parts and becomes like the original egg cell as happens in the division of a protozoan. However if the cells fail to remain united they do undergo a certain amount of regulation returning more or less to the condition of the egg; and if cell division is stopped differentiations quickly come to an end. In short it is necessary that the egg shall divide into many cells and that these cells shall remain in contact in order that differentiation may proceed; cell division is necessary to embryonic differentiation and cell union to organic integration. Multicellularity is thus one of the most important paths of progress that organisms have ever discovered.

2. *Multiplicity of Tissues, Organs and Parts.*—As multicellularity led to the possibility of differentiations between individual cells, so the grouping of similar cells together with their products into tissues, of tissues into organs, and of organs into systems has enormously increased the possibilities of differentiations among these parts. Within one of the higher animals or plants there are therefore many units of structure of varying degrees of complexity and among these there are innumerable numbers of differentiations while at the same time all are integrated into a single organism or person.

3. *Compound Organisms.*—Finally combinations of organisms known as corms, due to incomplete division, are found very generally in the plant kingdom and among the lowest animals such as sponges, hydrozoa, and polyzoa. Evidences of such incomplete division are found also in the segmentation of tapeworms, and in the metamerism of annelids, arthropods and vertebrates. In many of these cases this incomplete division makes possible a differentiation of the various zooids or segments so that as in the case of the hydrozoa one zooid may be nutritive in function and structure, another reproductive, another protective, etc. In metameric animals there may be a notable differentiation of different metameres; indeed in all the higher animals metameric differentiation is one of the

chief methods of bringing about increasing complexity of organization. Thus by the multiplication of cells, tissues, organs, systems, and zooids or metameres; by differentiations among the members of each of these classes; and by the integration of all of these into a single individual a degree of complexity of organization, both as to structure and function, is reached which so far as is known has no parallel elsewhere.

Just as some of the most complex protozoa represent the highest possible organization within the limits of a single cell so some of the most complex multicellular animals and plants represent the highest possible degree of organization within the limits of a single body. But no single animal or plant, however complex it may be, can combine within itself all the complexities of all organisms. The very nature of differentiation signifies limitations in certain directions in order to secure further development in other directions. If a vertebrate have wings it cannot also have hands (except in the artistic representation of angels) ; if it have limbs differentiated for running, it can not also have limbs specialized for swimming; if it have enormous strength it can not also have great delicacy of movement. Thus while certain animals are differentiated in one direction and others in another no one animal can be differentiated in all directions.

There is good reason to believe that multicellular organisms have already reached and in many cases passed the highest stage of organization which is possible within the limits of a single body. When differentiations in any one direction go so far that they unfit the organism for any condition of life except a single and special one the chances for survival are greatly reduced and sooner or later this highly differentiated organism becomes extinct or returns to a more generalized condition. Such limits to progressive differentiation have been reached in practically every group of animals and plants. The climax of the progressive evolution of fishes was reached in the Paleozoic Era, of amphibians in the Permian, of reptiles in the Mesozoic and of mammals in the Tertiary. In all these classes the formation of new species and genera has been going on throughout their entire history, there has been diversification and speciation without cessation, but progressive evolution in the sense of increasing complexity of organization has reached its limit.

In all existing classes of animals and plants progressive evolution has practically ended. Even in man, one of the latest products of evolution, there is evidence that physical and intellectual development have gone about as far as is possible; there

is not much prospect that the hand, the eye or the brain of man will ever be much more perfect than they are in many persons at present. It is of course conceivable that further evolution of the brain for example may occur, just as it is possible to conceive of a further evolution of the neck of the giraffe or of the trunk of the elephant, but there is a practical limit beyond which it is not possible to go. Differentiations must not go farther or faster than integrations and they must not render their possessor less fit to survive. It is very doubtful whether the brain of man could undergo much further differentiation without introducing disharmonies within the organism or with the environment.

Both in complexity of organization and in perfection of adaptation progress has always been most rapid at first and has then gone slower and slower until it stopped. It may be compared to a curve which rises rapidly at first and then approaches more and more to a straight line. Or better still it may be compared to a flow of lava which rushes forward while it is at a white heat and fresh out of the crater but goes more and more slowly as it cools until it stops altogether; if the central stream remains fluid (or the organism remains labile and relatively undifferentiated) it may burst out and again flow rapidly in one direction or another until it again cools and stops. Probably the farthest possible limits of progressive evolution have already been reached in all well-tried lines of progress. Further progress must be made in new lines if at all.

Among animals no new phyla have appeared since the vertebrates in the Silurian or perhaps even earlier; no new classes since the mammals in the Triassic and the birds in the Jurassic. In the evolution of animals only about fourteen times in the whole history of life have new phyletic paths been found and several of these were practically blind alleys and led nowhere, not even to the production of many species, as, for example, the ctenophores, the rotifers and the chætognaths. Apparently, therefore, the progressive evolution of multicellular organisms has come to an end so far as increasing complexity of organization of individuals is concerned.

4. *Social Evolution.*—Just as a great advance was entered upon when the path of multicellularity was taken, so a still greater advance was made possible when solitary forms entered upon the path of social organization. There are many grades of individuality in the living world from the visible and even the invisible parts of cells to whole cells, cell-aggregates, tissues, organs, systems, persons, corms, and finally colonies

and states. There are many grades of organization from the bacterium to the vertebrate, from the germ cell to the man. Animal societies are the last and highest grade of organization which has yet appeared on earth. In such societies the integration and cooperation of individuals makes possible a higher degree of differentiation than has ever appeared before, and the degree of differentiation of individuals which is possible is directly proportional to the extent of their integration.

The evolution of animal societies may be traced from a condition in which every member is much like every other and the bond of connection between individuals is a very loose one, up to societies of ants, bees and termites in which the specialization of individuals is higher, the mutual dependence more complete, and the work which the colony is able to perform is immensely greater and more perfect than could be accomplished by any number of individuals working separately. What the individual cannot do because of weakness, lack of differentiation and short life, the social group can accomplish with the strength and specialization of all and through long periods of time.

Whether social evolution, in which instincts alone are the integrating factors, has reached its highest possible development in colonies of ants, bees and termites no one can say, but it is certain that any further evolution along this line must lead to greater differentiation and integration of the constituent individuals, or of entire colonies.

5. *Rational Evolution of Human Society.*—Finally with the development of intelligence man has entered upon a new path of evolution in which progress has been extraordinarily rapid, namely the path of rational cooperation. All animal societies are based upon gregarious instincts and these instincts form the only bond of integration in most of these societies, but in man they are supplemented by intelligence and upon these gregarious instincts as a foundation rational cooperation has erected that enormous structure which we call civilization.

It is a notable fact that the social evolution of man has been very much more rapid than his physical evolution. In physical organization man has changed but little since the beginning of recorded history but in social organization the most enormous advances have been made and changes are still going on at a rate which is amazing if not alarming. The chief reason for this difference in the rate of physical and social evolution is to be found in the fact that experiences are more quickly registered in the intellect than in bodily structure or even in the in-

stincts, and that in intelligent social groups all past experiences may be transmitted to future generations, so that each new generation stands as it were on the shoulders of the preceding ones. On the other hand so far as bodily structures, functions and instincts are concerned, each generation begins life anew as germ cells and if it inherits any characters due to the experiences of its ancestors they are few and rare.

Conclusion

Finally if the rate of *divergent evolution* depends upon the number of mutations which appear, it should be proportional, other things being equal, to the rate of reproduction. But this as we have seen is not the case. If the rate of *adaptative evolution* depends upon the rate of mutation and the severity of elimination it also should be proportional to the rate of reproduction. On the other hand, some of the most highly adapted forms such as birds and mammals have a relatively low rate of reproduction. If all members of a phylum have evolved from a common ancestor those which have gone farthest in any line of adaptation must have gone fastest; but in general the most highly adapted forms have a low rate of reproduction. If the rate of *progressive evolution* depends upon the rate of mutation and the severity of selection it also should be proportional to the rate of reproduction, but it is at once apparent that this is not the case; the most complex and most highly differentiated of all animals have the lowest rate of reproduction.

These considerations lead one to seriously inquire whether recent theories as to the causes of evolution are wholly satisfactory. The rapid rate of evolution in active and highly complex but slow-breeding animals would be readily explained on Lamarckian principles. It seems highly probable that the rate of mutation is influenced by environmental conditions, as Plough has shown in the case of the pomice fly, and it is probable that environment has played a large part in the rate of evolution. On the other hand, the evidences against the inheritance of the effects of use or disuse are so strong that one hesitates to invoke their aid. Nevertheless a broad view of the past evolution of life upon the earth, of evolutionary diversity, adaptation and progress, and especially considerations of the rate of evolution, cause one to inquire whether there may not be other important factors which possibly are not yet "dreamed of in our philosophy."